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L.—*On the Cretaceous Fish Plethodus.* By A. SMITH WOODWARD, F.L.S., of the British Museum (Natural History).

[Plates XIII. & XIV.]

IN his well-known work on the 'Geology and Fossils of Sussex' (1850) Frederic Dixon briefly described and figured some remarkable crushing-teeth or dental plates from the Sussex Chalk, to which he gave the name of *Plethodus*. He compared them with *Ptychodus*, and referred them to the Cestraciant sharks. Numerous specimens were subsequently discovered both in the Chalk and Cambridge Greensand, a few also in the Gault of Folkestone; and when I was occupied with a general survey of the English Cretaceous fish-fauna in 1887 I prepared several sections to demonstrate their microscopical structure. It was proved that beneath the thick dense layer of vertical tubules of dentine observed by Dixon there was an equally thick base of true bone with numerous typical bone-lacunæ. The problematical fossils could not therefore be retained any longer among the Elasmobranchii. They were referred to some undetermined bony fish; and one small specimen in the Willett Collection in the Brighton Museum was mentioned as displaying the *Plethodus*-plate "so placed in the midst of a skull as to suggest its connexion with the pharyngeal bones"\*. During the last

\* A. S. Woodward, "A Synopsis of the Vertebrate Fossils of the English Chalk," Proc. Geol. Assoc. vol. x. (1888) p. 331.

twelve years I have searched in vain among English Cretaceous fish-remains for further evidence on the subject. The time seems therefore to have arrived for describing the scanty fragments of *Plethodus*, so far as they are known, in the hope that this or allied genera may soon be more satisfactorily elucidated by some of the collections of Cretaceous fish-remains which are now being made in other parts of the world.

The type specimen of *Plethodus expansus*\*, now in the Willett Collection, Brighton Museum, is part of the side of a large dental plate probably resembling the original of Pl. XIII. fig. 1 in size and shape. The slightly sinuous but generally convex grinding-surface does not exhibit any punctations, and consists of a thin, yellowish, opaque layer covering the thick agglomeration of parallel vertical tubes of dentine, which form the main mass of the plate. There is a base, presumably of bone, beneath this mass, but it seems to be comparatively thin. The lateral border of the plate is somewhat truncated, and it may have borne a few blunt tubercles, but this is not quite certain.

The specimen thus briefly described was obtained from the Middle Chalk of Malling, Sussex; but the dental plate most closely resembling it in the British Museum (Pl. XIII. fig. 1) is one of a considerable series of more or less abraded examples from the Cambridge Greensand. It is much battered and also scratched by small boring organisms; but it is evidently almost complete. It measures about 0.10 m. in length by 0.075 m. in maximum breadth, and is bilaterally symmetrical. The broader end is gently rounded, and three quarters of the length of the plate in this direction rise to a gentle median convexity. The other end tapers to a point, and its oral face is concave. The grinding-surface of the tooth is not punctate; its truncated lateral border is covered with rather large obtuse tubercles, which are not coated with ganoine or gano-dentine (fig. 1 a). The bony base of the dental plate is almost completely obscured by matrix, but where its lower face is exposed it exhibits very fine reticular markings, the main lines being longitudinal, the numerous less conspicuous cross-lines being at right angles to these. This reticulation is still more distinct on a fragmentary specimen from the Cambridge Greensand (Brit. Mus. no. 35392).

\* The type species, Dixon, *op. cit.* p. 366, pl. xxxiii. fig. 2. For the loan of this and other specimens in the Brighton Museum I am indebted to the kindness of Henry Willett, Esq., F.G.S., and Edward Crane, Esq., F.G.S.

The more abraded and imperfect specimens of the same dental plate from the Cambridge Greensand (*e. g.* Brit. Mus. no. P. 7274) exhibit a distinctly punctate crown, the punctations usually bordered by a raised rim. These evidently depend upon the structure of the thin, opaque, superficial layer of the tooth, but are only evident when the outermost surface is destroyed.

The thick translucent layer of vertical dentine-tubules is always distinct in broken sections of the plates; and when the bony base is also preserved, this is seen to have a vertically fibrous structure curiously resembling that of the dentine, but much finer. Sometimes, indeed (*e. g.* Brit. Mus. no. 39103), appearances have been mistaken to indicate two dental plates, one resting on the other. The fibrous bony base is, in fact, nearly as thick as the crown, and there is a sharp plane of demarcation between these two parts, which are sometimes not completely in contact, but exhibit a small interposed cavity.

At the same horizons as these slightly convex leaf-shaped dental plates there occur somewhat concave plates of similar structure, which seem to represent the opposing dentition. They are, indeed, commonly labelled *Plethodus expansus* in collections. An imperfect specimen from the Lower Chalk of Glynde in the Brighton Museum (Willetts Coll. no. 152) is broken across, exposing the characteristic dentine and basal bone, while its abraded oral face is punctate. It appears as if it had been bilaterally symmetrical, and from the middle of one end of the base there projects part of a fibrous azygous bony bar for an attachment of some kind. The bar is not seen at the other end, where, however, there is some indication of a paired connexion with adjoining bones. A more fragmentary specimen of the same plate with incomplete border is shown of two thirds the natural size in Pl. XIII. figs. 2, 2 *a*, 2 *b*. This was obtained from the Lower Chalk of Kent, and is now in the British Museum. It is remarkably concave and must have been originally about as broad as long. Its oral face (fig. 2) is not punctate, but the marginal area is covered irregularly with numerous shallow pits. The truncated border (fig. 2 *b*) is tuberculated, as in the leaf-shaped plates, and the median bony bar (*p*) at one end, noted in the previous specimen, is especially well preserved, though still incomplete. The form and direction of this bar are shown in figs. 2, 2 *b*, while adjoining it on each side in a nearly parallel plane there are remains of a comparatively thin lamina of bone (*x*) of uncertain form. The attached face of the dental plate, so far as exposed, has the curious

aspect shown in fig. 2 *a*. The reticular lines already described on the base of the leaf-shaped plates are here most prominent in a transverse direction, and pass into a remarkable cluster of vermiculating fibres on the median longitudinal ridge. This ridge does not extend to the ends of the plate; and at the end opposite to that where the bony process appears the ridge terminates at the apex of a bilaterally-symmetrical triangular area, on which the reticular markings exhibit chiefly a divergent fan-shaped arrangement. Another imperfect abraded specimen of the same plate (Brit. Mus. no. 39091), exposed from its aboral face, shows that the terminal bony bar is a tolerably thin lamina directly continuous with the bony base and apparently similar to the latter in texture (fig. 3).

There is much variation in the contour of the plates of both kinds commonly referred to *Plethodus expansus*, but it seems best at present not to separate them under distinctive names. Perhaps the most striking variation is observed in the convex plate from the Gault shown of two thirds the natural size in Pl. XIII. fig. 4. Both ends of this fossil are comparatively truncated and the sides are nearly parallel; but in general aspect it closely agrees with the typical form from the Cambridge Greensand represented in Pl. XIII. fig. 1.

Some small convex plates from the English Lower Chalk, however, seem to be quite distinct from *P. expansus*, and it is now proposed to describe them under the new specific name of *P. pentagon*. The type specimen (Pl. XIII. fig. 5) from the Lower Chalk of Burham, Kent, is imperfect at one angle, where the section displays the dentinal structure characteristic of the genus. The plate is longer than broad, pentagonal in outline, pointed at one end, truncated and slightly excavated at the other end. The abraded oral face, with punctate markings, is very gently convex and slightly curved upwards at the two sharp angles bounding the truncated end. Three pits or depressions occur on the oral face near this end. The steep lateral border is not tuberculated. A fragment of the pointed end, also from Burham (Pl. XIII. fig. 6), bears numerous pits or depressions on the attenuated point. Much-abraded specimens from the Lower Chalk of Dover (Brit. Mus. no. 35874) and Lewes (Brit. Mus. no. P. 2693) are only of interest as extending the known distribution of the species.

The Lower Chalk also yields a concave dental plate which might serve very well for the opposing dentition of *P. pentagon*, though, as only detached specimens have been

discovered, its determination must still remain uncertain. The best plate of this form in the British Museum is shown of the natural size in Pl. XIII. figs. 7, 7 *a*. It is strongly arched transversely, less so longitudinally, and a broken section at one end shows the characteristic structure. The oral face is not abraded, and is thus not punctate; it is deeply pitted at the lateral borders, which curve downwards to the coarsely tuberculated margin.

It may be observed that a somewhat similar form of dental plate, to be regarded as representing an allied species, *P. furcatus*, is known from the Turonian of Bohemia †.

A fourth form of dental plate referable to *Plethodus* is of comparatively small size, only 0·021 m. in length and 0·013 m. in maximum width. It is a unique specimen from the Lower Chalk of Clayton, Sussex, now in the Brighton Museum (Willett Coll. no. 153), and is described by Dixon under the name of *P. oblongus* (*op. cit.* p. 366, pl. xxxii.\* fig. 4). It is gently rounded at its wider end, almost truncated at the narrower end, and the whole of the oral face is gently convex.

This specimen is of great interest because it seems to be closely similar to the rounded end of a thick dental plate mingled with the remains of a small problematical skull from the same pit, also in the Brighton Museum (Willett Coll. no. 154). In fact there can be little doubt that the latter fossil is referable to *Plethodus*, whether its determination as *P. oblongus* be right or wrong. There is thus at last some clue to the nature of the fish to which the dental plates under consideration belong. It is only strange that the first evidence as to the characters of the skull should appear in connexion with the smallest species, and not in association with the larger plates, which must have been connected with a very massive bony skeleton.

The imperfect skull in question is shown of the natural size from both sides in Pl. XIV. figs. 1, 1 *a*. The cranium is much laterally compressed and about as deep as long, with a very steep frontal profile. At first sight, indeed, it exhibits much resemblance to that of the extinct Pycnodont fishes. The cranial roof-bones have a peculiar fibrous and punctate structure, and some of the sutures between them are distinguishable on the right (fig. 1). At the postero-lateral angle above the hyomandibular (*hm.*) the squamosal element is distinct (*sq.*), but its upper limit posteriorly is not quite clear. Adjoining the anterior half of its upper border there is a

† *Chimæra furcata*, A. Fritsch, 'Reptilien und Fische der böhmischen Kreideformation' (1878), p. 16, woodcut. Referred to *Plethodus* by A. S. Woodward, Proc. Geol. Assoc. vol. x. (1888) p. 331.

transversely elongated narrow bone, tapering as it reaches the broken median crest of the cranium; and this may probably be interpreted as a parietal (*pa.*) meeting its fellow in the median line. There may perhaps be a small supra-occipital crest (*x*), but this is uncertain. In front of the squamosal and supposed parietal only one bone can be distinguished forming the rostral region, and this probably consists of the pair of frontals fused with the mesethmoid. Postero-laterally, where in contact with the hinder elements, the bone exhibits radiating fibres like an ordinary frontal membrane-bone (*fr.*), but further forwards it becomes finely punctate and rugose. Two facettes on the border above the position of the orbit are probably for the overlap of the two membrane-bones noted in the next specimen. The upper part of the frontal profile is compressed to a sharp edge, but further down it displays a slight flattened concavity, while the extremity of the snout is broken away. A small depression on the surface of the undoubted frontal bone seems to represent a mucus-pit (*m.*). The basicranial axis, so far as preserved (to the border of the hyomandibular), is straight and parallel with the ridge of the cranial roof behind the frontal angle. Its constitution is uncertain, but as a median vertical lamina seems to extend from its upper face to meet the excessively developed mesethmoidal plate (*m.eth.*), the part preserved may possibly be a much-extended vomer (*v.*) like that of the Pycnodonts. It expands below the position of the eye and forms a thickened plate, which is distinctly concave on its oral face. The fossil is unfortunately cracked along the middle of this face, and the plate cannot be very satisfactorily studied; but it bears an extraordinary resemblance to the concave plates of *P. expansus* described above (p. 355, Pl. XIII. fig. 2), while its aboral face, especially on the left side (fig. 1 *a, u*), exhibits the peculiar fine reticulation already noted on the detached specimens. It must, however, be admitted that the peculiar dentinal structure so characteristic of *Plethodus* cannot be distinctly observed. Of the mandibular suspensorium, the very deep and narrow hyomandibular (*hm.*) is shown on each side, with a prominence on its thickened hinder border for the suspension of the operculum. The mandible (*d*) is rather fragmentary, but shown on the right side to be comparatively short and deep, implying a rather small gape. The right dentary bears minute, obtuse, styliform teeth on the border, apparently arranged in more than one series, while part of the inner face of the left dentary displays the surface of attachment for a dense cluster of minute teeth (*t*). Below the hinder end of

the mandible on the left side there is displayed one end of a comparatively thick convex dental plate (*h*), which has precisely the aspect of that of *Plethodus* both outwardly and in transverse section. It is not fixed upon bone, and may well have belonged to the hyoid arch. On the left side the preoperculum (*p.op.*) is shown to be very large and widely expanded at its angle. The operculum (*op.*) is only represented by a fragment.

A second example of this type of skull, in some respects more satisfactory, is preserved in the British Museum (no. 49895). This fossil, from the Lower Chalk of Dorking, Surrey, displays only the left side of the head, and is shown of the natural size in Pl. XIV. fig. 2. The same form of cranium is readily distinguishable; but the squamosal element is imperfect, the lateral margin of the frontal region is bounded by a postfrontal (*pt.fr.*) and a prefrontal (*pr.fr.*) membrane-bone, while the mesethmoid terminates in front in a thickened obtusely pointed rostrum (*r.*), which is ornamented with close reticulating ridges and lines of tubercles \*. There are also two small plates posteriorly (*s.t.*) which may, perhaps, be supratorpals. The frontal (*fr.*) exhibits the mucus-pit (*m.*) as before, and it seems to cover only the hinder part of the rostral region, though its apparent boundaries in the fossil are probably deceptive and due to accidental cracks. The mesethmoidal septum (*m.eth.*) is seen to meet a vertical plate rising from the basicranial axis, and the latter exhibits the same remarkable expansion as in the previous specimen. At least this seems to be the case, for there is evidence of crushing in this region, and a longitudinal ridge along the supposed basicranial expansion is probably the fractured and slightly displaced base of the vertical plate just mentioned. In a plane distinctly external to the expansion there are remains of the hyomandibular (*hm.*) and the pterygo-quadrate arcade; the metapterygoid (*m.pt.*), quadrate (*qu.*), and long slender ectopterygoid with its minute teeth (*ecpt.*) being readily distinguishable. Indeed, if the previous specimens were unknown the expansion itself might readily be interpreted as entopterygoid, while the ridge upon it would be considered as an accidentally crushed and displaced slender parasphenoid. The maxilla (*mx.*) is a deep laminar bone, finely tuberculated at its oral margin, which forms the greater part of the upper border of the mouth. The premaxillæ are

\* It may be noted that this rostrum exhibits much resemblance to a comparatively large tip of a snout from the Sussex Chalk, once provisionally assigned to an Acipenseroid fish (A. S. Woodward, Proc. Geol. Assoc. vol. xi. 1889, p. 31, pl. i. fig. 6).

unknown, but may be fused with the short ornamented rostrum, which curves inwards to the mouth below and seems to bear minute teeth. The mandible, as before, is shown to be short and deep, the dentary (*d.*) forming by far the greater part of the ramus. A fragment within the jaws may possibly be part of the lower dental plate, but it is unusually pitted and of doubtful nature. The operculum (*op.*) and the curved anterior border of the preoperculum (*p.op.*) are also seen.

The evidence afforded by the two skulls now described is thus very suggestive, but not quite conclusive as to the relationships of the dental plates named *Plethodus*. It is still necessary to demonstrate by microscopical sections that the plates in this small form of skull are truly *Plethodus*. It is also essential to obtain a clearer view of the basicranial axis before definitely deciding upon the homologies of the upper plate. Meantime, however, it seems almost certain that the concave plate of *Plethodus* was part of the upper dentition fixed to the basicranial axis, while the convex plate belonged to the lower dentition and was supported by the hyoid apparatus. The upper plate may have been part of the parasphenoid—an arrangement common among fishes—or it may have belonged to a much-extended vomer like that of the extinct *Pycnodonts*.

There is only one difficulty in regarding the concave plate of *P. expansus* as homologous with the upper plate in the small form of skull now described, namely that the aboral face is a little different. The median ridge in the known specimens of *P. expansus* does not definitely rise into a vertical plate, though this may have been comparatively fragile and readily broken away; moreover, in the larger plate the strongest lines in the fine reticulation on either side of the median ridge are directed transversely, while those in the original of Pl. XIV. fig. 2 are longitudinal. It is, however, possible that accident in the first case and specific difference in the other may account for the discrepancy. If the homology prove to be well founded, it is likely that the end of the plate connected with the ascending bar of bone (Pl. XIV. fig. 2, *p*) is posterior.

Finally, assuming that the new type of skull now described does really represent the genus *Plethodus*, it is still difficult to hazard a suggestion as to the precise affinities of the fish. The structure of the mandible shows that it is not a *Pycnodont*, while the apparent discovery of a hyoid or lingual dentition opposed to the upper dentition of the mouth adds a feature not previously known among Mesozoic fishes. The dental arrangement, indeed, is most closely similar to that of



some of the existing Osteoglossidæ, a family which was already differentiated in the Eocene in North America (*Dapedoglossus*) and probably also in Europe (*Brychætus*). If the patches of minute teeth on the parasphenoid and basi-hyal of the recent *Arapaima* were fused together into opposing plates their structure would not be very different from that of *Plethodus*. The disposition of the squamosal and parietal bones in the Cretaceous fish limits comparisons to primitive bony fishes such as the Osteoglossidæ, Elopidae, and Albulidæ. On the whole, I am inclined to think that *Plethodus* will eventually prove to be most closely related to the first of these families.

## EXPLANATION OF THE PLATES.

## PLATE XIII.

- Fig. 1.* *Plethodus expansus*, Dixon; lower dental plate, oral face, two thirds nat. size, and view of tuberculated rim (1 *a*), nat. size.—Cambridge Greensand. [B.M. no. 35369.]
- Fig. 2.* Ditto; upper dental plate, oral face, aboral face (2 *a*), and side view of supposed posterior end (2 *b*), two thirds nat. size.—L. Chalk; Kent. *p*, median bony process; *r*, lateral bony plate. [B.M. no. 38585.]
- Fig. 3.* Ditto; upper dental plate, aboral face, two thirds nat. size.—Ibid. [B.M. no. 39091.]
- Fig. 4.* Ditto (?); lower dental plate, oral face, two thirds nat. size.—Gault; Folkestone. [B.M. no. P. 7.]
- Fig. 5.* *Plethodus pentagon*, sp. n.; lower dental plate, oral face.—L. Chalk; Burham. [B.M. no. 41716 *a*.]
- Fig. 6.* Ditto; pointed end of plate, oral face.—Ibid. [B.M. no. 47947.]
- Fig. 7.* Ditto (?); upper dental plate, oral face, and lateral aspect (7 *a*).—English Chalk. [B.M. no. P. 5626.]

## PLATE XIV.

- Fig. 1.* *Plethodus oblongus*, Dixon (?); imperfect head, right and left (1 *a*) lateral aspects.—L. Chalk; Clayton. [Willett Coll., Brighton Museum, no. 154.]
- Fig. 2.* Ditto; imperfect head, left lateral aspect.—L. Chalk; Dorking. [B.M. no. 49895.]

*d.*, dentary of mandible; *ecpt.*, ectopterygoid; *fr.*, frontal; *h*, lower dental plate (? basihyal); *hm.*, hyomandibular; *m.*, mucus-pit; *meth.*, mesethmoid; *met.*, metapterygoid; *mx.*, maxilla; *op.*, operculum; *pop.*, preoperculum; *pa.*, parietal; *pr.fr.*, prefrontal plate; *pt.fr.*, postfrontal plate; *qu.*, quadrate; *r*, rostrum; *s.t.*, supratemporals (?); *sq.*, squamosal; *t*, inner mandibular teeth; *u*, upper dental plate; *x*, supraoccipital (?).

B.M.=British Museum. Unless otherwise stated, the figures are of the natural size.